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Light intensity affects leaf morphology in a wild population of *Adenostyles alliariae* (Asteraceae)

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Abstract

Low light conditions can impose environmental stress on plants, and plants often respond adaptively by increasing their leaf area. Light stress on plants can also result in developmental instability, which can manifest as increased fluctuating asymmetry in leaves or other organs. The relationship between light conditions and fluctuating asymmetry has been documented in experimental populations, but has been less frequently observed in the wild. Here, we studied how leaf surface area and fluctuating asymmetry correlate with light intensity in a wild population of *Adenostyles alliariae* (Asteraceae). We found strong evidence that leaf surface area increases and weak evidence that fluctuating asymmetry increases as light intensity decreases. Our results help to elucidate the relationship between light stress and developmental instability under naturally occurring conditions.

Keywords

fluctuating asymmetry, light intensity, developmental instability, phenotypic plasticity, *Adenostyles alliariae*

Introduction

Plant growth and survival are strongly influenced by abiotic factors such as light intensity, nutrient availability, and temperature (Agarwal et al. 2006). These abiotic factors can produce conditions that are unfavourable for normal plant development (Jan et al. 2012). Plants living in shaded or poor nutrient habitats or in areas outside their optimal temperature ranges can display increased levels of stress compared to plants

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living in more favourable environments (Sridevi et al. 1999; Lynch and Brown 2001; Yang et al. 2019). To survive in these stressful environments, plants have evolved the ability to respond to abiotic stressors with physiological and morphological alterations (Alpert and Simms 2002), resulting in intraspecific phenotypic variation (Miner et al. 2005; Rozendaal et al. 2006).

Plants require light for their development and metabolism, but they sometimes occur in areas where light availability is below the optimum level (i.e., light stress, Niinemets 2010; Cramer et al. 2011; Zhu et al. 2017). In these conditions, plants often respond by increasing their leaf area to intercept more sunlight (Dwyer et al. 2014; Liu et al. 2016), although this response can vary even among closely related species (Sultan 2003). As a result, plants growing in different natural light conditions are expected to have different leaf sizes (Marques et al. 1999).

Another consequence of light stress for plants is a phenomenon known as developmental instability (DI). DI occurs when an organism is unable to achieve its developmentally programmed phenotype, and can result from unfavourable environmental conditions (Markow 1995). One common manifestation of DI is fluctuating asymmetry (FA), or small deviations from perfect symmetry in otherwise symmetrical structures (Moller and Shykoff 1999; Cornelissen and Stiling 2010). These deviations are caused when organisms are exposed to severe stress at certain critical development stages, resulting in abnormal phenotypes and increased phenotypic variability among individuals (Waddington 1956; Graham et al. 1993). FA can reflect disturbances in developmental homeostasis at the molecular, chromosomal or epigenetic levels (Parsons 1990). Because FA is easily measured in the field, it is often used as a surrogate for DI in ecological studies (Palmer and Strobeck 1986; Graham et al. 2010). In studies of DI resulting from light stress in plants, researchers have often focused on FA in the leaves (Midgley et al. 1998; Roy and Stanton 1999; Venâncio et al. 2016).

If leaf FA is greater at low light intensity, this might be because low light intensity causes developmental stress. Alternatively, the relationship might be mediated by leaf growth. If leaves in low light conditions are larger than leaves in high light conditions, then they must grow faster or for longer, and faster or longer growth might result in DI (Moller and Eriksson 1994; Cuevas-Reyes et al. 2011). These potential drivers of FA have not been fully disentangled.

In the Carnic Alps, the herbaceous perennial *Adenostyles alliariae* (Asteraceae) is a useful model for investigating DI in response to light conditions. The species is common and grows in both coniferous forests and alpine meadows, and therefore occupies habitats with a wide variety of light conditions. Phenotypic variation and DI have not yet been examined in this species. Additionally, light stress is one of the most uncharacterized and least studied abiotic stresses that plants encounter (Yang et al. 2019). In this study we investigated both phenotypic variation and DI of *A. alliariae* leaves in areas of differing sunlight exposure. We measured phenotypic variation using leaf area, and used leaf FA as a surrogate for DI (Santos et al. 2013). We hypothesised that leaves growing in low light conditions would have increased area and increased FA, which may indicate phenotypic compensation for low light conditions and increased levels of stress in *A. alliariae*, respectively.

Methods

Site selection

Fieldwork was conducted at the Baita Torino field station in the Passo del Pura, Ampezzo, Friuli-Venezia Giulia, Italy (46°25.5433'N, 12°44.5167'E (DDM), 1400 m asl) between 11:00 and 13:00 on 9, 11 and 12 July 2019. The area is part of the Carnic Alps, which are characterised by high plant biodiversity and endemism (Pignatti and Pignatti 2014). We selected four study sites in the vicinity of the Baita Torino. Two sites (i.e., the shaded sites) were covered by coniferous forest (primarily *Abies alba* and *Picea abies*) and two sites (i.e., the open sites) were unforested. Sites were selected for their coverage properties and for the presence of *A. alliariae*. Thus, site selection was not random.

Data collection

At each site we randomly selected 25 individual *A. alliariae* plants with no signs of herbivory for study (i.e., 100 plants in total). We identified the most basal leaf on each plant and we measured the light intensity at its apex and base, and on the right and left side of the leaf at its widest points using the Google Science Journal application (version 3.2) on an iPhone 7. We averaged these measurements to estimate the light intensity reaching the leaf. We then collected the leaf and photographed it on a white background with a 25 mm scale bar. We used ImageJ (version 1.51) to measure the adaxial surface area of each leaf. We also measured the distance from the midrib to the widest points on the left and on the right sides of the leaf. We called these distances *Ls* and *Rs*, respectively (Figure 1). We estimated the directed asymmetry, d, of each leaf using $d = \log(Ls) - \log(Rs)$ (Waddington 1960; Venâncio et al. 2016). Thus, $d > 0$ if $Ls > Rs$ and $d < 0$ if $Ls < Rs$. This measure is unitless and depends on the shape but not on the size of the leaf. We estimated the undirected asymmetry of each leaf as $|d|$ (Waddington 1960; Venâncio et al. 2016). The undirected asymmetry captures the magnitude but not the direction of asymmetry in each leaf.

Analyses

Asymmetry in a population can be fluctuating or directional. Directional asymmetry occurs if one side of an organ or organism is consistently different from the other in all members of a population, and need not indicate DI (Graham et al. 1993). For example, in Tengmalm's owl (*Aegolius funereus*), the right ear aperture is positioned higher on the head than the left, and this is believed to enhance directional hearing (Norberg 1978). In our study, asymmetry would be directional if the left side of the leaf were consistently larger than the right side, or vice versa. To test for directional asymmetry, we applied a one-sample t-test to ask whether d was significantly different from zero.

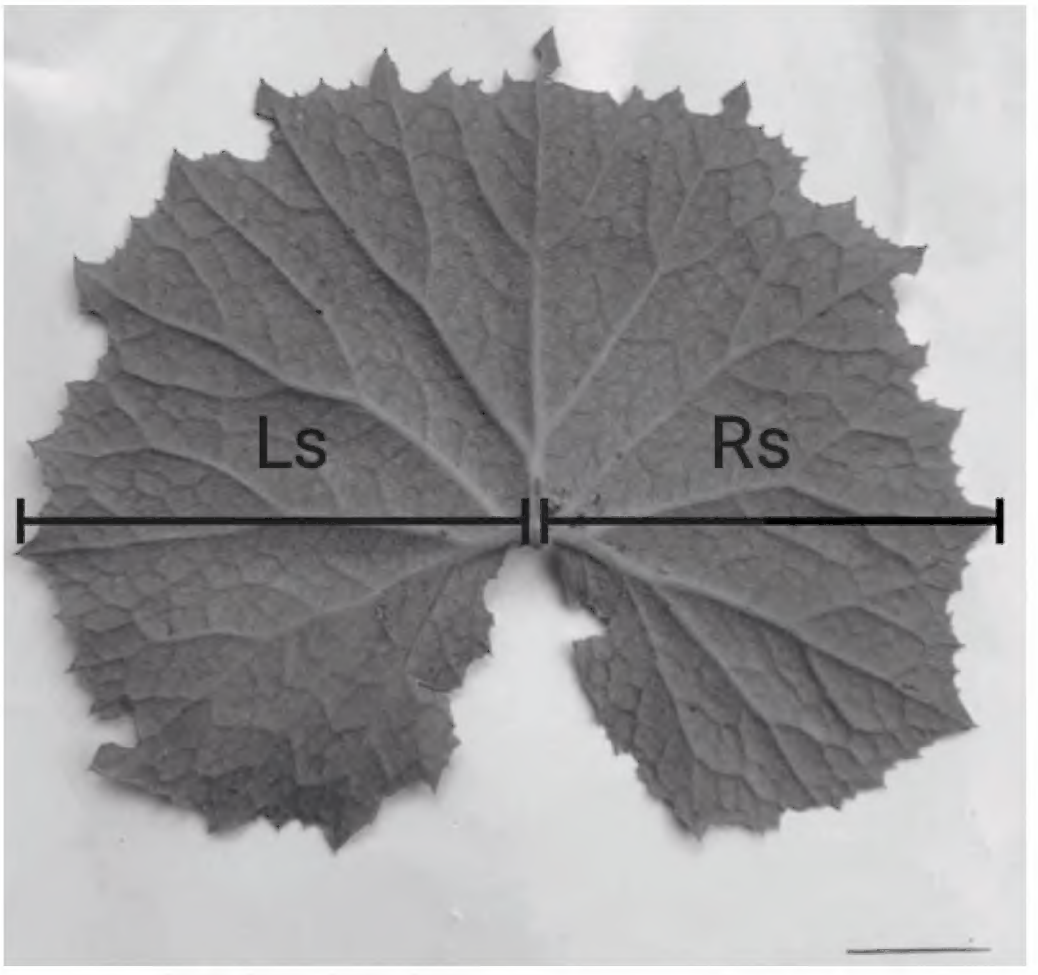

Figure 1. The most basal leaf from an *A. alliariae* plant sampled in this study. *Ls* and *Rs* represent the measures for the midrib to the widest points on left and right of the leaf, respectively.

In the absence of directional asymmetry, we can interpret the undirected asymmetry of leaves in our study as FA. We regressed the logged leaf area and FA on the logged light intensity reaching each leaf using mixed effects models implemented in the R package lme4 (Bates et al. 2015). The models included random effects of site (to account for potential differences in site qualities such as soil chemistry) and day (to account for systematic differences in light measurements due to weather on different days). The residuals of the fitted models were not normally distributed, so we Box-Cox transformed logged leaf area and FA (Box and Cox 1964; Venâncio et al. 2016) using the powerTransform function in the R package car (Fox and Weisberg 2019). Box-Cox transformation requires that data to be transformed be strictly positive, and our FA measurements included two zeros. Therefore, we Winsorised the zero values to the smallest non-zero value in the data set (i.e., the smallest FA we know we could detect, Tukey 1962) prior to Box-Cox transformation. Then, we refit the mixed effects models to the transformed data. We calculated p-values for the effects of logged light intensity on logged leaf area and FA using the Satterthwaite approximation (Satterthwaite 1941; Luke 2017) implemented in the R package lmerTest (Kuznetsova et al. 2017).

If the relationship between FA and light intensity is mediated by leaf growth, then under the same light conditions we would expect leaves that grow faster or for longer (i.e., larger leaves) to show more FA. Thus, we would expect to see a relationship between leaf area and FA after controlling for light intensity. To test this, we regressed Box-Cox transformed FA on logged light intensity and logged leaf area in a mixed

model with random effects of site and day, and estimated p-values using the Satterthwaite approximation.

Data are available in Suppl. material 1: File S1: aa_data.csv, and the R code used to analyze the data is available in Suppl. material 1: File S2: Francis_and_Gilman_analysis.R. Both files are also archived in the TRY Plant Trait Database (Kattge et al. 2011) at https://doi.org/10.17871/TRY.49.

Results

The light intensity measured at individual leaves varied within sites (Figure 2), but was higher overall at open sites (8.26 ± 0.22 log(lx)) than at shaded sites (6.75 ± 0.25 log(lx)) (Monte Carlo randomisation, $p < 0.0001$). The mean logged leaf area was 9.53 ± 0.07 log(mm^2) in open sites and 9.79 ± 0.07 log(mm^2) in shaded sites. The mean undirected asymmetry was 0.069 ± 0.005 in open sites and 0.080 ± 0.008 in shaded sites.

Adaxial surface area increased with decreasing light intensity ($p < 0.0001$, $\beta = -0.27$ log(mm^2) $log(lx)^{-1}$ calculated at the mean-centered logged light intensity of 7.50 log(lx); Figure 3A). We found no evidence that asymmetry in the study population was directional rather than fluctuating ($p = 0.2032$) and thus we treated undirected asymmetry as FA. We found weak evidence that FA increased with decreasing light intensity ($p = 0.0730$, $\beta = -4.8 \times 10^{-3}$ $log(lx)^{-1}$ calculated at the mean-centered logged light intensity; Figure 3B). If we forced site type (i.e., open or shaded) into the model, we found no relationship between site type and either logged leaf area ($p = 0.70$) or FA ($p = 0.99$). Thus, leaf morphology is better explained by light intensity at the individual leaf than by light intensity at the study site. We found no relationship between FA and logged leaf area after controlling for the effect of light intensity ($p = 0.532$). Therefore, we have no evidence that the effect of light intensity on FA was mediated by leaf growth.

Discussion

Plants can respond to environmental stresses by modifying their physiology and morphology, and this is reflected in their phenotypic variation (Miner et al. 2005; Rozendaal et al. 2006). Such modifications are common in plants growing in conditions of poor light availability (Markesteijn et al. 2007). In this study, we found that *A. alliariae* growing at lower light intensity produce larger leaves. A plastic response of leaf size to light intensity is likely to be adaptive for plants that experience variable light conditions between generations or across small spatial scales (Markesteijn et al. 2007).

We found weak evidence that leaf FA increases with decreasing light intensity in *A. alliariae*. The relationship between light intensity and FA has found mixed support in the literature. Several studies have reported increased leaf FA in plants growing at low light intensity under manipulated (*Sinapis arvensis* Roy & Stanton, 1999; *Quercus pyrenaica* Puerta-Pinero et al., 2008; *Silene vulgaris* Sandner & Matthies, 2017) or natural

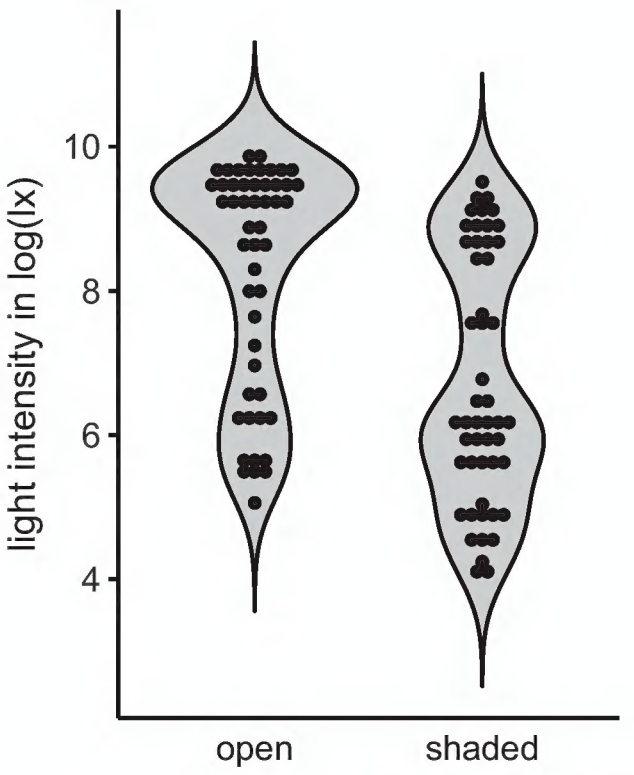

Figure 2. Light intensity measured at individual leaves in open and shaded sites.

conditions (*Quercus alba* Kusi, 2013; *Miconia fallax* Alves-Silva, 2012). In contrast, Wuytack and colleagues (2011) found no effect of light intensity on leaf FA in *Salix alba* and Venâncio and colleagues (2016) found no effect of light intensity on leaf FA in *Bauhinia brevipes*, albeit in a study of only 26 plants versus the 100 plants in our study. Other studies have found that FA increases with increasing light intensity. For example, Midgley and colleagues (1998) found that leaf FA in *Dimorphotheca sinuate* increased with UV-B exposure, although their UV-B exposure treatments simulated depleted ozone conditions and were therefore greater than plants regularly encounter. Tucic and Miljkovic (2010) found increased FA in *Iris pumila* growing higher light conditions in nature, but in flowers rather than leaves. To our knowledge, our study provides the first evidence of increasing FA with decreasing light intensity in a naturally occurring population of an herbaceous plant. Given the variability of reported results, systematic work to identify the ecological traits or genotypes that mediate the relationship between leaf FA and light intensity might reward effort.

Some authors have suggested that the relationship between low light intensity and increased leaf FA might be mediated by leaf growth (Moller and Eriksson 1994; Cuevas-Reyes et al. 2011). That is, leaves grow to greater size under low light conditions, and the demands of longer or faster growth might result in stress and thus developmental instability. However, if that were the case, we would expect larger leaves to show more FA under similar light conditions, and we did not see this pattern in our study. Many environmental conditions other than light can also affect leaf FA, and some of these conditions may have varied among sites in our study. However, we controlled for site-specific environmental variation by including site as a random effect in our analyses. Therefore, we believe that differences in light intensity are likely to explain the differences we observed in leaf FA among *A. alliariae* plants.

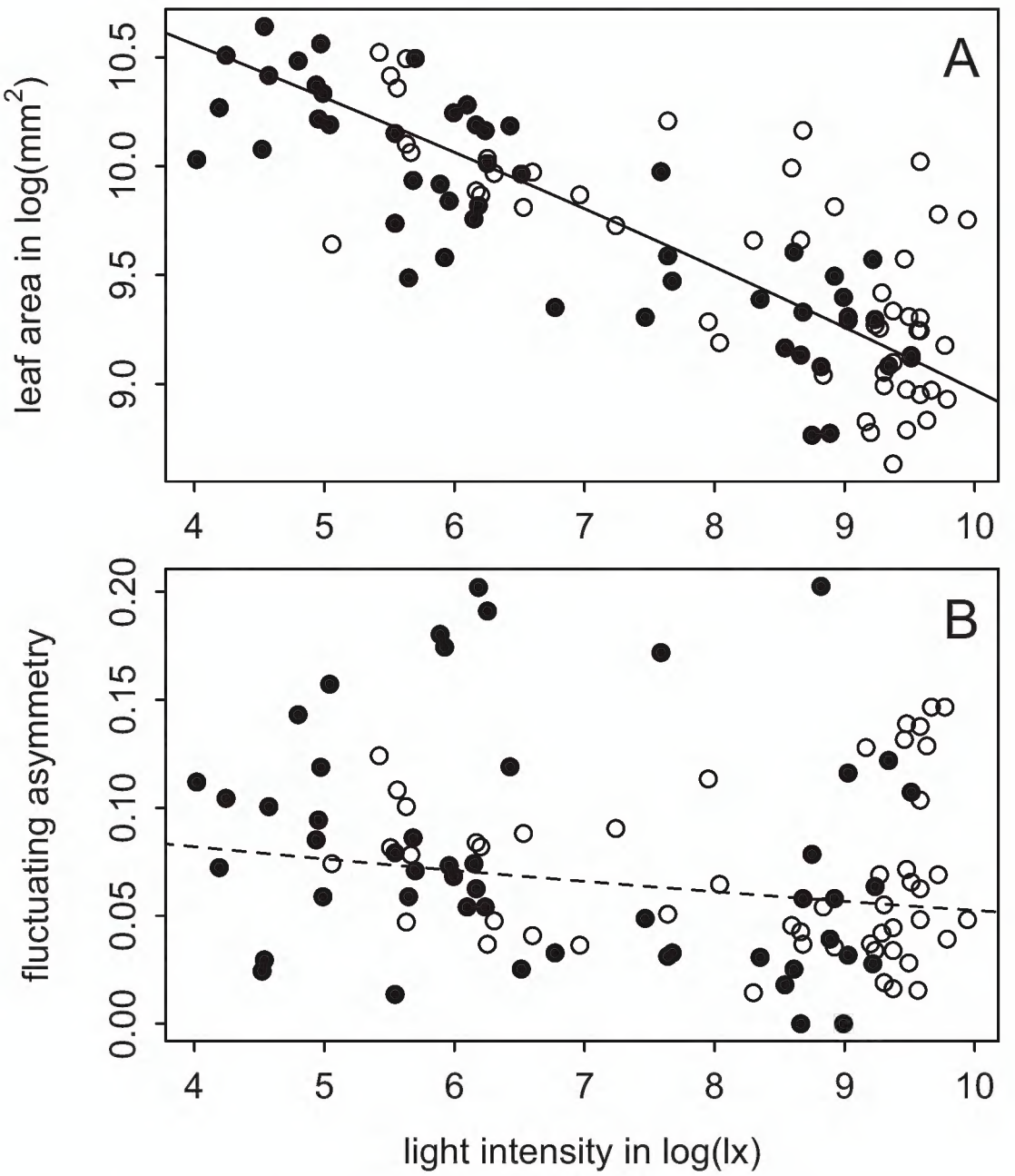

Figure 3. Effects of light intensity on adaxial surface area **A** and FA **B** in *A. Alliariae* leaves. Each point represents the most basal leaf of a plant growing in a shaded (filled circles) or open (open circles) site. The solid line indicates a significant relationship ($p < 0.0001$) and the dashed line indicates a marginally significant relationship ($p = 0.0732$). Lines of best fit are back-transformed from models fitted to Box-Cox transformed data.

Our study examined only one leaf per plant. Therefore, we cannot determine whether light intensity at each leaf affects the morphology of that leaf, or whether the light intensity experienced by each plant affects the morphology of all leaves on the plant and the light intensity at the most basal leaf is correlated with the light intensity experienced by the plant as a whole. These two possibilities are not mutually exclusive, and the answer need not be the same for leaf area and FA. Studies that assess the light intensity at and morphology of multiple leaves per plant could answer this question. To our knowledge, this analysis has rarely been attempted for FA (but see Kusi 2013).

A broad understanding of how light intensity affects developmental instability in plants remains to be achieved. By linking light intensity to fluctuating asymmetry in a naturally occurring population, albeit weakly, we believe our study offers a step toward that goal.

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Supplementary material 1

Supplementary files

Authors: Bailey Francis, Robert Tucker Gilma

Data type: morphometric data

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